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Applying crown and bole allometry to management of boreal mixedwood species

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Applying crown and bole allometry to management of boreal mixedwood species

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Abstract

The effectiveness of crown characteristics for estimating growth potential of boreal mixedwood species was tested, and allometry of crowns and boles was used to develop management recommendations. One thousand trees were destructively sampled in four mature boreal mixedwood stands in northwestern Ontario. Crown characteristics performed similarly to commonly reported competition indices in explaining tree growth variation, while avoiding drawbacks associated with developing and applying competition indices in boreal mixedwood stands. Live crown ratio (LCR) weighted by estimated crown fullness explained 36%, 53%, and 57% of diameter growth variation in black spruce (*Picea mariana* [Mill] B.S.P.), white spruce (*Picea glauca* [Moench] Voss), and balsam fir (*Abies balsamea* [L.] Mill.), respectively. Since crowns integrate competitive effects over several growing seasons, average crown characteristics may estimate productivity potential better than a competition index measured at a single point in time. Differences in mean crown characteristics, diameter growth efficiency, and slenderness coefficient among crown positions were often unique to each species, indicating a potential role for these measures in guiding management decisions. Species-specific recommendations appropriate for the sampled stands were proposed. More research is needed to develop tree allometry as a tool for large-scale management of diverse forest types.

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Introduction

The extent, persistence, inherent biological diversity, and increasing economic value of Canada's boreal mixedwood forests justify informed, sustainable management of mixed-species crops on appropriate sites (MacDonald 1995). Lieffers and Beck (1994) described the advantages of promoting mixedwood forests, concluding that future management systems will emphasize deliberate mixtures of species at the expense of single-species plantations. However, the amount of information regarding the effect of stand structure on productivity of component species in complex mixedwood forests is inadequate. Improved knowledge is essential to guide stand structure manipulation, through modified harvesting or pre-harvest treatments, to promote sustainable growth of desired species mixtures.

A variety of competition indices incorporating competitor abundance, proximity, and size have been used to estimate crop tree growth potential (Lorimer 1983, Pukkala 1989, MacDonald et al. 1990, Biging and Dobbertin 1992, Rouvinen and Kuuluvainen 1997). These indices typically include direct or indirect measurements of subject tree size, which may confound the effect of competition with the effect of inherently superior growth in larger subject trees. Furthermore, adequate sample sizes for index development are often obtained by treating each tree as both a subject tree and a competitor, but this approach violates the assumption of independence in statistical tests (Mitchell-Olds 1987, Cole and Lorimer 1994). Reliable competition indices are difficult to develop and apply in mixedwood stands because of structural complexity and physiological diversity (Gerrard 1969, Yoshida and Kamitani 2000, Goreaud et al. 2002). Since competition constrains rather than determines growth, any competition index is limited in its ability to predict crop tree performance (Burton and Dougherty 1993).

Some of the drawbacks associated with developing and applying competition indices in boreal mixedwood stands could be overcome by measuring characteristics of subject trees, rather than intensity of surrounding competition. For example, tree growth potential of component species could be estimated by quantifying their crown and bole characteristics, which integrate the effects of competition (Raulier et al. 1996, Rouvinen and Kuuluvainen 1997, Opio et al. 2000).

In this paper, allometry is defined as the proportional size relationship between two parts or attributes of a plant at a single point in time. Allometry of crowns and boles has long been used to describe the status of individual trees (Assmann 1970), but has not been widely applied to boreal mixedwood stand management. Relative tree dimensions have been used as indicators of wind damage risk, which is a serious concern after partial cutting on some boreal mixedwood sites (Navratil 1995, MacDonald 2000).

Trembling aspen (*Populus tremuloides* Michx.) is the main hardwood species in boreal mixedwood stands, and since it is a very shade-intolerant, aggressive pioneer species, it is managed under a simple even-aged silvicultural system (clearcutting) to regenerate fully stocked sucker-origin stands (Perala 1990). More uncertainty surrounds effective approaches for maintaining good growth of associated conifers, primarily black spruce (*Picea mariana* [Mill] B.S.P.), white spruce (*Picea glauca* [Moench] Voss), and balsam fir (*Abies balsamea* [L.] Mill.) (Drew 1988, MacDonald and Thompson 2003). These conifers are shade-tolerant (Baker 1949), developing slowly in the understory until released by a disturbance that removes all or part of the canopy. In northern Ontario, changes in natural disturbance patterns, primarily through expansion of clearcut harvesting, have favoured hardwoods and non-crop competitors at the expense of desirable conifers (Yang and Fry 1981, Hearnden et al. 1992).

The objectives of this paper are (1) to test the effectiveness of crown characteristics for estimating tree growth potential of the main boreal mixedwood species; and (2) based on differences in crown and bole allometry, to develop recommendations for managing component species in boreal mixedwood stands similar to those sampled in this study.

Methods

Study sites

Four fire-origin boreal mixedwood stands were selected in northwestern Ontario, Canada, between 48°25′ and 50°22′ N, and between 87°03′ and 90°12′ W. Age since disturbance ranged from 65 to 95 years. Canopies were dominated by trembling aspen, with scattered jack pine (*Pinus banksiana* Lamb.) and clumps of white birch (*Betula papyrifera* Marsh.). Younger cohorts of conifers, primarily black spruce

Table 1. Stand ages and basal areas at the study sites.

Site	Age (years)				Basal area ($m^2 ha^{-1}$)	
	Hardwoods		Conifers			
	Mean	SD[a]	Mean	SD	Hardwoods	Conifers
Boreal Road	63.6	12.9	54.1	15.2	12.5	9.2
Hanover Lake north	94.5	16.6	86.0	22.2	16.9	28.2
Hanover Lake south	62.6	7.9	51.2	9.0	24.8	13.3
Shebandowan Lake	78.4	30.8	48.7	16.0	9.8	8.2

[a]Standard deviation.

and balsam fir, occurred in lower-canopy positions. Soils were moderately deep, with fresh moisture regimes and predominantly loam textures (Ontario Institute of Pedology 1982). Stand ages and basal areas are compared among sites in Table 1.

Field measurements

At each site, a 0.20-ha circular plot was established. Within each plot, the species, crown position, and crown width (average of two perpendicular diameters) were recorded for every living tree with a diameter at breast height (DBH) greater than 1.0 cm. Crown position was classified as lower-, mid-, or upper-canopy, representing < 33%, 33 to 66%, or > 66% of the crown length receiving direct light, respectively. Crown fullness was also estimated to the nearest 5% by visualizing the degree to which each tree's foliage would fill a geometric solid (usually a cone or paraboloid) bounded by the crown surface. After felling, the basal age, height, and crown length of each tree were measured. The total sample size was 1000 trees.

The total lengths and two most recent increments were measured along two perpendicular radii of a breast-height disk removed from each tree. The outside-bark diameter was calculated by summing the two lengths, and the previous two diameter increments were calculated by summing the corresponding radial increments. The most recent increment was incomplete because trees were felled during the growing season. Thus, the penultimate diameter increment was used in the analyses.

Data analyses

For each sample tree, several allometric measures were derived: (1) diameter growth efficiency, by dividing DBH growth (mm) by crown width (m); (2) live crown ratio (LCR), by dividing crown length (m) by total height (m); (3) weighted LCR, by converting crown fullness to a proportion between 0 and 1, and multiplying it by LCR; (4) slenderness coefficient, by dividing total height (m) by DBH (m); and (5) crown shape ratio, by dividing crown width (m) by crown length (m).

Diameter growth efficiency is a simpler version of two analogous measures: volume growth efficiency, which expresses volume or biomass growth per unit leaf area (Jack et al. 2002, Xiao et al. 2003); and the index of growing space economy, which expresses volume growth per unit of projected crown area (Hamilton 1969, Assmann 1970). Slenderness coefficient is commonly used as an index of susceptibility to wind damage (Navratil 1995, Wang et al. 1998). Crown shape ratio (Larocque and Marshall 1994), also termed "crown fullness ratio" (Assmann 1970), provides an alternative index of wind damage risk and a basis for relative density prescriptions among species.

The square root of annual DBH growth was regressed on unweighted and weighted LCR, using eq. 1 and eq. 2, respectively:

$$[1] \quad (\Delta DBH)^{0.5} = \beta_0 + \beta_1(LCR) + \varepsilon$$

$$[2] \quad (\Delta DBH)^{0.5} = \beta_0 + \beta_1(LCR \cdot CF) + \varepsilon$$

where CF is crown fullness, β_0 and β_1 are the intercept and regression coefficient, respectively (estimated by ordinary least squares regression), and ε is the error term. Separate regressions were conducted for black spruce, white spruce, balsam fir, and trembling aspen. Since residual analyses revealed heteroscedasticity in all cases, the square root of DBH growth was used as the dependent variable to stabilize the variance. Regression estimates of DBH growth at low and high levels of unweighted and weighted LCR were compared among species.

To help assess allometric responses, diameter growth efficiency, LCR, crown fullness, slenderness coefficient, and crown shape ratio were compared among species and crown positions. To identify differences among species, Tukey's Honestly Significant Difference test for unequal sample sizes was applied to means within each crown position. Tukey's test is conservative, identifying fewer significant differences and maintaining a lower type I error rate than other common multiple comparison procedures (Dowdy and Wearden 1983).

Statistica® 6.0 (StatSoft Inc., Tulsa, OK) was used for all statistical tests and graphics.

Results

Growth estimation

Regressions of DBH growth over unweighted and fullness-weighted LCR were significant at $p < 0.001$ (Table 2). For conifers, weighted LCR produced higher regression coefficients and adjusted r^2 values and lower standard errors. For trembling aspen, unweighted LCR produced the better fit. However, the adjusted r^2 value associated with unweighted LCR for aspen was lower than the values associated with weighted LCR for conifers. Figs. 1 and 2 illustrate the effect of weighting LCR on the growth relationship for each species.

With weighted LCR, black spruce had the lowest regression coefficient and adjusted r^2 value among the conifer species. Average DBH growth was greater in aspen than in associated conifers at low and high LCR levels (Table 3). For conifers with low weighted LCR, growth was greatest in balsam fir and least in white spruce. At a high level of weighted LCR, growth was greatest in white spruce and least in black spruce.

For upper-canopy trees, diameter growth efficiency was greatest in trembling aspen and least in black spruce (Table 4). For mid- and lower-canopy trees, it

Table 2. *Regression statistics for relationship between annual growth in diameter at breast height (ΔDBH) and live crown ratio (LCR) unweighted and weighted by crown fullness (CF), by species.*

		Unweighted LCR[a]					Weighted LCR[b]				
Species	N	β_0	β_1	Adj. r^2	SEE[c]	p	β_0	β_1	Adj. r^2	SEE	p
Black spruce	320	0.393	0.947	0.187	0.249	<0.001	0.429	1.306	0.359	0.221	<0.001
White spruce	51	0.045	1.807	0.235	0.371	<0.001	0.193	2.457	0.528	0.291	<0.001
Balsam fir	401	0.268	1.423	0.377	0.317	<0.001	0.599	1.534	0.574	0.262	<0.001
Trembling aspen	228	0.504	2.900	0.268	0.445	<0.001	1.082	1.858	0.122	0.488	<0.001

[a] Regression equation: $(\Delta DBH)^{0.5} = \beta_0 + \beta_1(LCR) + \varepsilon$, where β_0 and β_1 are the intercept and regression coefficient, respectively, and ε is the error term.

[b] Regression equation: $(\Delta DBH)^{0.5} = \beta_0' + \beta_1(LCR \ CF) + \varepsilon$, where β_0 and β_1 are the intercept and regression coefficient, respectively, and ε is the error term.

[c] Standard error of estimate.

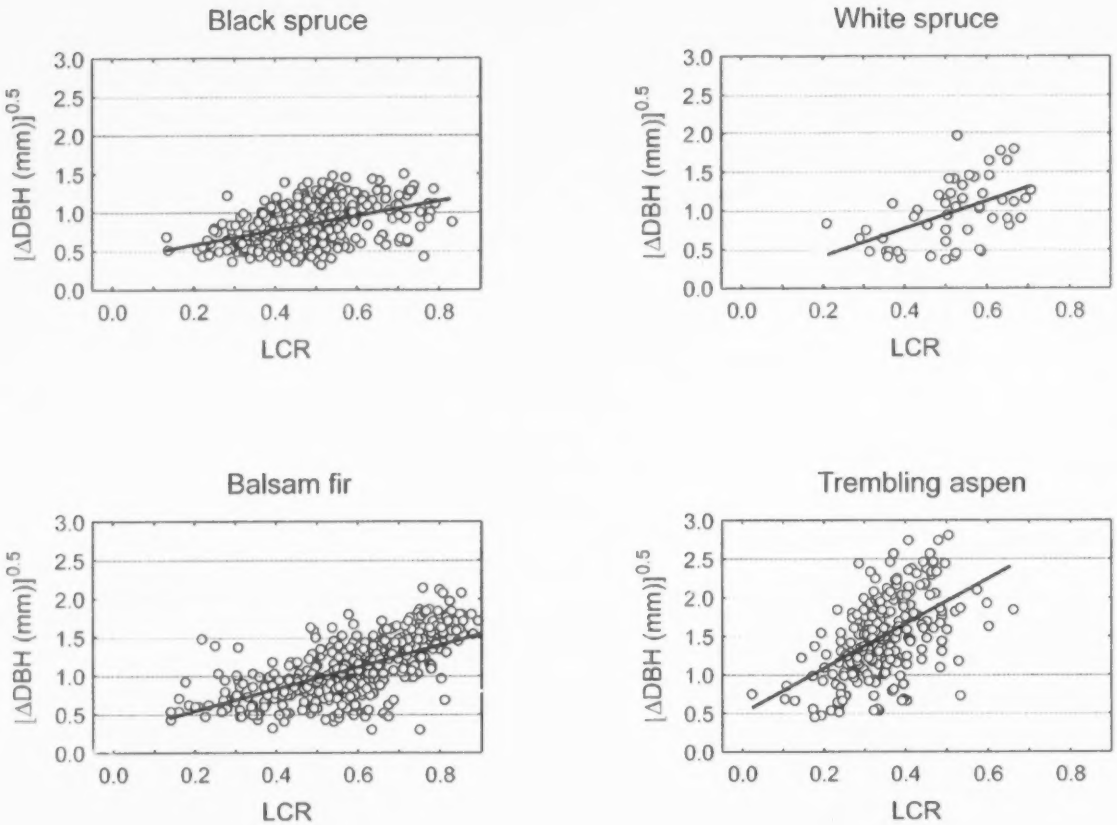

Figure 1. *Relationship between transformed diameter at breast height (DBH) growth and live crown ratio (LCR) for the main boreal mixedwood species.*

was greatest in balsam fir and least in the spruces. Although diameter growth efficiency generally declined with decreasing crown position, in balsam fir it was greater for mid- and lower-canopy trees than for upper-canopy trees.

Crown and bole allometry

In every species, LCR was similar among crown positions (Table 5). LCR was greatest in balsam fir, but differences among species lessened as crown position decreased. Within each crown position, crown fullness was similar among species, especially for conifers (Table 6). As crown position decreased, the rate of decline in crown fullness was greater than the rate of decline in LCR. Both indices declined relatively more in trembling aspen than in the other species. However, inferences are tentative because there were only four data points for lower-canopy aspen. By definition, lower-canopy aspen trees are rare in boreal mixedwood stands because aspen is a shade-intolerant pioneer species that does not persist in the understory (Perala 1990). As crown position decreased, LCR declined more in white spruce than in black spruce or balsam fir. Although LCR declined little in black spruce, crown fullness declined more in this species than in the other conifers. Crown fullness declined relatively less in balsam fir than in any other species.

For all crown positions, slenderness coefficient was greatest in black spruce and trembling aspen, and did not differ significantly between white spruce and balsam fir (Table 7). In all species, slenderness coefficient increased as crown position decreased. Crown shape ratio also increased as crown position decreased, but black spruce crowns were consistently narrowest (Table 8).

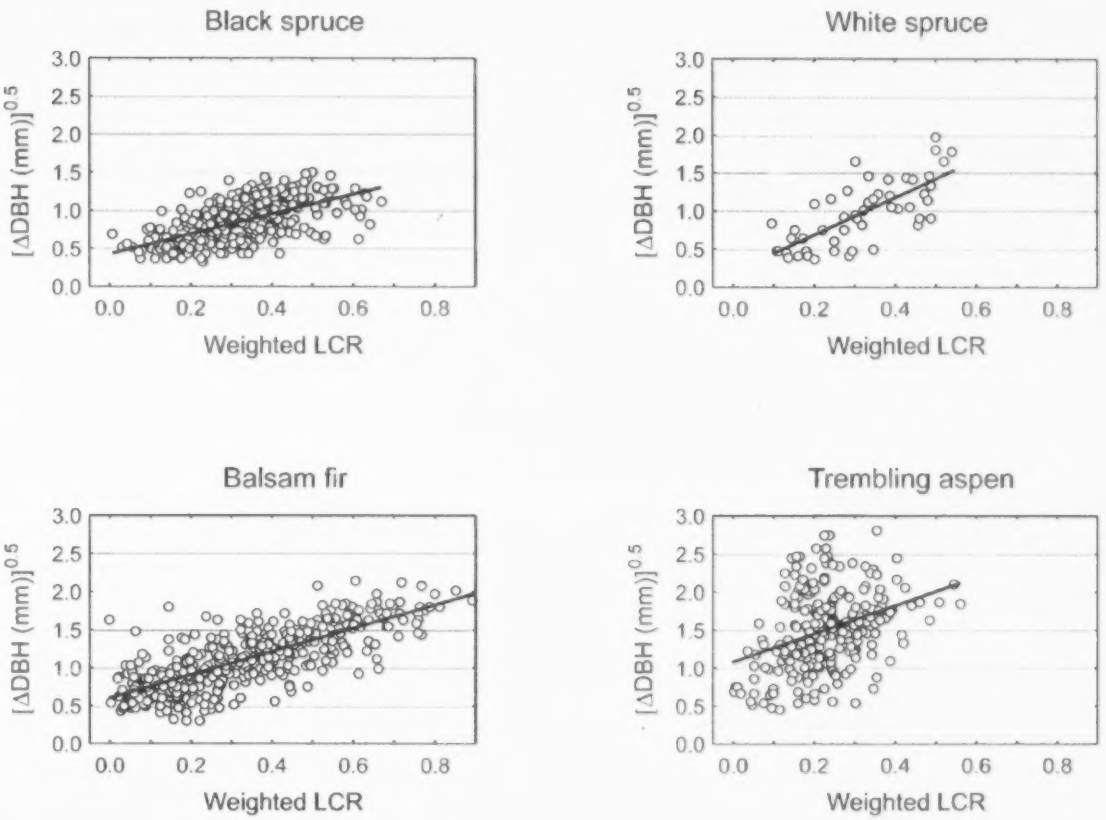

Figure 2. *Relationship between transformed diameter at breast height (DBH) growth and live crown ratio (LCR) weighted by crown fullness for the main boreal mixedwood species.*

Discussion

Growth estimation

Competition indices generally explain less than 50% of subject tree growth variation (Pukkala 1989, Hasenauer 1993, Brandeis et al. 2001, Duchesneau et al. 2001), especially when subject tree size is not included in the index. In this study, LCR performed comparably to reported competition indices, with unweighted LCR explaining 27% of trembling aspen diameter growth, and weighted LCR explaining 36% to 57% of conifer diameter growth (Table 2). Furthermore, LCR is more easily acquired for operational management decisions because it does not require size and proximity measurements of neighbouring competitors.

Weighted LCR quantified two main elements of crown status: (1) relative size, which differed most among species (Table 5); and (2) relative foliage content, which differed most among crown positions (Table 6). Hasenauer (1993) reported that subject tree LCR is the main driver in growth models of mixed Norway spruce (*Picea abies* L. Karst) and common beech (*Fagus silvatica* L.) stands. Larsen (1994) included a crown recession function in a stand dynamics model, claiming that changes in crown characteristics of crop trees and competitors must be quantified to obtain accurate growth projections. The results of other studies on a variety of species suggest that relative crown size and vigour are effective estimators of tree growth potential (Smith and Long 1989, Biging and Dobbertin 1992, Cole and Lorimer 1994, Raulier et al. 1996, Ruel et al. 2000a, Duchesneau et al. 2001).

Trembling aspen had a relatively high standard error of estimate associated with its growth—LCR relationship, reflecting the variable crown characteristics of deliquescent hardwoods, compared to the more precisely quantifiable crown characteristics of excurrent conifers. Black spruce's

Table 3. *Comparison of annual growth in diameter at breast height (ΔDBH) among species at low and high levels[a] of live crown ratio (LCR) unweighted and weighted by crown fullness (CF).*

	Estimated ΔDBH (mm)			
	Unweighted LCR[b]		Weighted LCR[c]	
Species	Low (0.20)	High (0.60)	Low (0.10)	High (0.50)
Black spruce	0.339	0.924	0.313	1.171
White spruce	0.165	1.275	0.192	2.021
Balsam fir	0.305	1.258	0.566	1.866
Trembling aspen	1.175	5.036	1.607	4.044

[a]Selected levels differed between unweighted and weighted LCR according to actual data ranges.

[b]Based on the regression equation: $(\Delta DBH)^{0.5}=\beta_0+\beta_1(LCR)+\varepsilon$, where β_0 and β_1 are the intercept and regression coefficient, respectively, and ε is the error term.

[c]Based on the regression equation: $(\Delta DBH)^{0.5}=\beta_0+\beta_1(LCR\ CF)+\varepsilon$, where β_0 and β_1 are the intercept and regression coefficient, respectively, and ε is the error term.

low regression coefficient and adjusted r^2 value indicated that diameter growth may be less affected by crown characteristics in this species than in white spruce or balsam fir. Since black spruce crowns were relatively narrower than those of other species (Table 8), variations in LCR and crown fullness would result in smaller variations in leaf area, and hence potential growth. In contrast, a species whose growth responds well to changes in crown extent (e.g., white spruce) should be spaced adequately to optimize crown development.

Trembling aspen growth was more than triple or double that of the best-producing conifer species, based on estimates with unweighted and weighted LCR, respectively (Table 3). These results support the view that aspen displays aggressive growth throughout its range, and has a pronounced ability to express dominance over neighbouring trees (Perala 1990). The growth rate of aspen is generally greater than that of associated species on boreal sites (Reich et al. 2001, Pothier and Prevost 2002). Aspen establishes immediately after wildfire in boreal mixedwood forests of northern Quebec, with spruce and fir regeneration following after approximately five years (Bergeron and Charron 1994). Aspen rapidly attains dominance, while other species remain in lower-canopy positions. Although total yield may be enhanced by maintaining a high proportion of aspen, a more salient challenge is to manage the hardwood and conifer components to attain target species mixtures appropriate for regional mill demands.

Trembling aspen had greater absolute growth than the other species, regardless of LCR level (Table 3). However, in mid- and lower-canopy positions, balsam fir had greater diameter growth efficiency than the other species (Table 4). Since fir grew better than black spruce or white spruce when crowns were poorly developed (Table 3), it appears to be a good candidate for managing as a lower-canopy or understory species. Fir is the most shade-tolerant boreal mixedwood species (Baker 1949), and attains its full growth potential at less than half of full sunlight, while black spruce requires full sunlight (Logan 1969). Furthermore, maintaining fir as a subordinate species in mixed stands minimizes damage by the spruce budworm (*Choristoneura fumiferana* Clemens) (Su et al. 1996).

Although white spruce was the least productive conifer when crowns were poorly developed, it had greater DBH growth than black spruce or balsam fir when crowns were well developed (Table 3). This was confirmed by white spruce's diameter growth efficiency ranking, which was last among conifers for lower-canopy trees, but first for upper-canopy trees (Table 4). Thus, lower-canopy white spruce should be released early enough to permit full crown development.

Table 4. Diameter growth efficiency[a], by species and crown position.

Species	Upper-canopy N	Upper-canopy Mean[b]	Upper-canopy SD[c]	Mid-canopy N	Mid-canopy Mean	Mid-canopy SD	Lower-canopy N	Lower-canopy Mean	Lower-canopy SD
Black spruce	98	0.34_{A}	0.14	201	0.26_{A}	0.19	21	0.27_{AB}	0.23
White spruce	11	0.55_{AB}	0.30	23	0.38_{AB}	0.20	17	0.20_{A}	0.16
Balsam fir	41	0.46_{A}	0.22	145	0.62	0.28	215	0.55_{B}	0.42
Trembling aspen	184	0.68_{B}	0.46	40	0.42_{B}	0.38	4	0.46_{AB}	0.20

[a] ΔDBH/CW, where ΔDBH is annual growth in diameter at breast height (mm) and CW is crown width (m).

[b] Within each crown position, means with the same subscript letter do not differ significantly at p=0.05 (Tukey's Honestly Significant Difference test for unequal sample sizes).

[c] Standard deviation.

Black spruce may not be the preferred conifer component in boreal mixedwood stands, since it produced only about 60% of the diameter growth of white spruce or balsam fir at high levels of weighted LCR (Table 3). Furthermore, its diameter growth efficiency was low in all crown positions (Table 4). If black spruce crop trees are desired, high densities of this species should be maintained to compensate for slow growth of individual trees.

Crown and bole allometry

As crown position decreased, crown development of all species declined (Tables 5 and 6). Crown fullness was more responsive than LCR to decreasing crown position, which reflects constraints on foliage development in shaded conditions. Species differences in mean crown characteristics and morphological responses to crown position were consistent with results reported elsewhere (Kubota and Hara 1996, Williams et al. 1999, Yoshida and Kamitani 2000). These differences suggest a role for crown measurements as indicators of the relative growth potential of associated species in diverse stand structures.

In western Canadian boreal mixedwood stands, slenderness coefficients exceeding 100 are associated with high wind damage risk (Navratil 1996). In this study slenderness coefficients indicated that black spruce and trembling aspen could sustain more wind damage than white spruce or balsam fir following partial cutting (Table 7). Wang et al. (1998) also found that slenderness coefficients for black spruce and aspen exceeded those for white spruce. Since aspen is seldom managed as a residual species following partial cutting, potential wind damage is an issue primarily for black spruce.

Wind damage risk is indicated by slenderness coefficient, which quantifies bole allometry. Windthrow risk may also be a function of root system morphology. In general, black spruce, white spruce, and balsam fir develop shallow root systems that exploit organic horizons, and aspen develops deeper lateral and sinker roots in mineral horizons (Strong and La Roi 1983). White spruce and balsam fir had the lowest slenderness coefficients, but their shallow root systems increase their susceptibility to windthrow after release (MacDonald 2000, Ruel et al. 2000b). In all species, the increase in slenderness coefficient as crown position decreased indicated that lower-canopy trees are vulnerable to wind damage and thus should be released in stages rather than in a single, heavy partial cutting. Holbrook and Putz (1989) also reported increased slenderness coefficients and decreased mechanical stability in suppressed trees.

Crown shape ratio indicates risk of wind breakage and windthrow by quantifying the ability of the crown to transmit wind forces to the bole. Although black spruce's high slenderness coefficient implied a susceptibility to wind breakage, its relatively narrow crown (Table 8) provides a smaller target for wind forces relative to crowns of other species. Trembling aspen is likely more susceptible to wind damage

Table 5. *Live crown ratio[a], by species and crown position.*

Species	Upper-canopy N	Upper-canopy Mean[b]	Upper-canopy SD[c]	Mid-canopy N	Mid-canopy Mean	Mid-canopy SD	Lower-canopy N	Lower-canopy Mean	Lower-canopy SD
Black spruce	98	0.48	0.11	201	0.47_{A}	0.13	21	0.46_{AB}	0.16
White spruce	11	0.60_{A}	0.07	23	0.53_{A}	0.10	17	0.43_{AB}	0.12
Balsam fir	41	0.64_{A}	0.12	145	0.64	0.15	215	0.55_{B}	0.19
Trembling aspen	184	0.36	0.09	40	0.31	0.09	4	0.18_{A}	0.07

[a] CL/H, where CL is crown length (m) and H is total height (m).

[b] Within each crown position, means with the same subscript letter do not differ significantly at p=0.05 (Tukey's Honestly Significant Difference test for unequal sample sizes).

[c] Standard deviation.

because it had high values of both slenderness coefficient and crown shape ratio. White spruce and balsam fir had low-risk slenderness coefficients compared to black spruce (Table 7), but their relatively wider crowns may transmit greater wind forces to their boles (Table 8). In all species, the increase in crown shape ratio as crown position decreased paralleled the trend in slenderness coefficient, confirming that lower-canopy trees are vulnerable to wind damage after release.

Information on crown shape ratio can also be used to guide density prescriptions for coexisting species (Philip 1994). Based on its narrow crown form, black spruce should be maintained at greater densities than white spruce or balsam fir. Conversely, in upper- and mid-canopy positions, trembling aspen should be managed at wider spacings than its associated conifers. Elevated crown shape ratios in lower-canopy trees (Larocque and Marshall 1994) suggest low density prescriptions for these cohorts.

Dominant hardwoods typically develop wide crowns, diverting resources to maintain branchwood at the expense of bolewood. Conifers lack the crown plasticity and gap-filling ability of hardwoods (Bond 1989). For example, the crown expansion rate of yellow birch (*Betula alleghaniensis* Britt.) in gaps is eight times that of Fraser fir (*Abies fraseri* (Pursh) Poir.) or red spruce (*Picea rubens* Sarg.) (White et al. 1985).

The productivity of hardwood-dominated stands could be increased by introducing conifers such as black spruce, which have low crown shape ratios. Shade-tolerant conifers efficiently convert resources to usable wood by occupying gaps or understory niches among hardwoods. Species mixtures are most effectively managed as vertical strata, with the most shade-intolerant species in the overstory (Smith et al. 1997). Yokozawa and Hara (1995) suggested that an arrangement of hardwoods over conifers is geometrically compatible because the centre of foliage mass is high in the former and low in the latter. Combining species with different crown forms may increase volume growth by 10 to 15%, compared to pure stands of any component species (Pukkala et al. 1994).

The presence of many small sun flecks increases the rate of oscillation of light intensity, a condition that favours photosynthesis (Barkman 1992). Thus, trees under small-leaved species, such as spruce or fir under trembling aspen, can photosynthesize at low average light intensities. Aspen has small leaves that oscillate rapidly with air movement, enhancing photosynthetic conditions for understory conifers.

Small saplings have a better chance of surviving under a dense canopy than do larger pole-sized individuals because maintenance respiration costs of living cells increase dramatically with tree size (Waring 1991). Thus, mixtures of conifer and hardwood species tend to develop canopy strata, with conifers remaining in the lower canopy or understory to minimize maintenance costs until a gap arises.

Table 6. Crown fullness[a], by species and crown position.

Species	Upper-canopy N	Upper-canopy Mean[b]	Upper-canopy SD[c]	Mid-canopy N	Mid-canopy Mean	Mid-canopy SD	Lower-canopy N	Lower-canopy Mean	Lower-canopy SD
Black spruce	98	74.0_{A}	12.5	201	64.4_{A}	15.0	21	37.1_{A}	17.3
White spruce	11	75.9_{AB}	14.3	23	65.4_{A}	14.4	17	44.4_{A}	9.3
Balsam fir	41	66.1_{AB}	16.5	145	62.3_{A}	19.6	215	43.8_{A}	21.7
Trembling aspen	184	67.7_{B}	18.3	40	56.8_{A}	19.5	4	10.8_{A}	8.1

[a]Degree to which foliage fills a geometric solid bounded by the crown surface (%).

[b]Within each crown position, means with the same subscript letter do not differ significantly at p=0 05 (Tukey's Honestly Significant Difference test for unequal sample sizes).

[c]Standard deviation.

Allometric relationships as management tools

Diameter growth was positively and uniquely related to relative crown extent in each species. Thus, where stand structure data are unavailable, crown allometry can be used to help plan productive combinations and spatial orientations of species. Crown characteristics are easily measured, and in this study were as effective as many commonly reported competition indices in explaining growth variation. Since crowns integrate competitive effects over several growing seasons (Raulier et al. 1996, Takahashi 1996, Rouvinen and Kuuluvainen 1997, Maguire et al. 1998), average crown characteristics may provide a better estimate of tree growth potential than a competition index measured at a single point in time. Furthermore, a reliable competition index is difficult to develop and test in boreal mixedwood stands, which have inherently complex species compositions and stand structures (Goreaud et al. 2002).

Differences in crown and bole allometry among species can be used to develop guidelines for boreal mixedwood management. For example, allometric relationships suggested the following management implications for the stands sampled in this study:

1. White spruce and balsam fir have more potential than black spruce for enhanced growth by managing for improved crown characteristics.
2. Trembling aspen outproduces its associated conifer species at all live crown ratios.
3. Lower-canopy and understory cohorts should be adequately spaced to permit their lateral crown expansion.
4. When conifers will be managed for extended periods in the lower canopy or understory, balsam fir should be more productive than black spruce or white spruce.
5. If maintained in an upper-canopy position, white spruce is a more efficient wood producer than black spruce.
6. On an individual-tree basis, black spruce is not an efficient wood producer compared to white spruce or balsam fir. However, it can be managed at higher densities, and its crown form makes it less susceptible to wind damage following stand opening.
7. Lower-canopy trees of all species are vulnerable to wind damage following canopy removal, indicating that low-intensity partial cutting should be considered to protect residuals.

Allometry is presented here as a tool for guiding forestry practices to optimize relative positioning of component species in boreal mixedwood stands. It could also be applied to stand yield determinations by including density or ground cover estimates of various tree strata (Assmann 1970).

More research is needed to determine how crown and bole allometric relationships are affected by specific management practices throughout stand development. The feasibility of applying remotely sensed imagery of crown and bole characteristics to boreal mixedwood management should also be investigated.

Table 7. *Slenderness coefficient[a], by species and crown position.*

Species	Upper-canopy N	Upper-canopy Mean[b]	Upper-canopy SD[c]	Mid-canopy N	Mid-canopy Mean	Mid-canopy SD	Lower-canopy N	Lower-canopy Mean	Lower-canopy SD
Black spruce	98	104.3	14.0	201	109.6	17.6	21	127.9_{A}	20.2
White spruce	11	74.0_{A}	17.1	23	92.3_{A}	13.6	17	101.0_{B}	15.1
Balsam fir	41	75.9_{A}	13.7	145	96.8_{A}	15.3	215	98.2_{B}	17.6
Trembling aspen	184	94.1	21.7	40	127.4	16.9	4	135.2_{A}	10.5

[a] H/DBH, where H is total height (m) and DBH is diameter at breast height (m).

[b] Within each crown position, means with the same subscript letter do not differ significantly at p=0 05 (Tukey's Honestly Significant Difference test for unequal sample sizes).

[c] Standard deviation.

Table 8. *Crown shape ratio[a], by species and crown position.*

Species	Upper-canopy N	Upper-canopy Mean[b]	Upper-canopy SD[c]	Mid-canopy N	Mid-canopy Mean	Mid-canopy SD	Lower-canopy N	Lower-canopy Mean	Lower-canopy SD
Black spruce	98	0.32_{A}	0.10	201	0.39	0.10	21	0.61_{A}	0.31
White spruce	11	0.39_{AB}	0.10	23	0.52_{AB}	0.14	17	0.92_{A}	0.33
Balsam fir	41	0.42_{B}	0.14	145	0.44_{A}	0.18	215	0.90_{A}	0.47
Trembling aspen	184	0.56	0.18	40	0.56_{B}	0.17	4	0.65_{A}	0.03

[a] CW/CL, where CW is crown width (m) and CL is crown length (m).

[b] Within each crown position, means with the same subscript letter do not differ significantly at p=0.05 (Tukey's Honestly Significant Difference test for unequal sample sizes).

[c] Standard deviation.

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